Madroño, Vol. 51, No. 3, pp. 280–286, 2004

TEMPORAL VARIATION IN LONGEVITY OF *OPUNTIA ENGELMANNII* (CACTACEAE) FLOWERS

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Abstract

Flower longevity interacts with other variables such as pollinator visitation and plant resources to control fruit set and seed production of many flowering plants. This study examined temporal patterns of floral longevity for *Opuntia engelmannii* Salm-Dyck. (Engelmann prickly-pear), a shrubby cactus common in the northern Sonoran Desert. Observations made at Tumamoc Hill, Tucson, AZ, USA, demonstrated that the flowers can open on a single day or two consecutive days. On average, one-day flowers opened at 1100 hr and closed 5.5 hr later at 1630 hr (MST). Flowers that bloomed on two consecutive days were open altogether for an average of 12.2 hr. Their first day of bloom lasted about 6.5 hr, beginning around 1000 hr and ending at about 1630 hr; on their second day, two-day flowers opened at 0830 hr and closed shortly after 1400 hr. The proportion of two-day flowers in the population was inversely related to maximum temperature on the first day of bloom and minimum temperature between the first and second days of bloom. Flowers opening in the afternoon were more likely to bloom a second day than those opening in the morning. Flowers open for the second time offered significantly less nectar and pollen than freshly opened flowers; nevertheless, rewards on the second day were high enough to encourage visitation by potential pollinators. Patterns of daily opening and closing appeared well suited to reducing the risk of poor or no pollination.

Resumen

La longevidad de flores se relaciona con otros factores como visitas de polinizadores y recursos de la planta para regular la produccíon de frutas y semillas. Esta investigacíon examina los patrones temporales de longevidad en flores de *Opuntia engelmannii* Salm-Dyck. (el nopal de Engelmann), un cactus común del norte del Desierto Sonorense. Observaciones en Tumamoc Hill, Tucson, Arizona, EEUU, demostran que las flores se abren un o dos días. Flores que abren por solo un día abrieron a las once de la mañana y cerraron a las cuatro y media de la tarde. Las que florecen por dos días seguidos se quedaron abiertos por un promedio de 12.2 horas en total. Su primer día de floracíon duró ~ 6.5 horas, comenzando a más o menos las diez de la mañana y terminando a más o menos las quatro y media de la tarde. En su segundo día las flores de dos días abrieron a las ocho y media de la mañana y cerraron poco después de las dos de la tarde. El porcentaje de las flores de dos días en la poblacíon esta relacionado inversamente con la temperatura máxima en el primer día de floracíon y la temperatura mínima entre los dos días de floracíon. Las flores que abren por la tarde fueron más probables de durar dos días que ésas que abren por la mañana. Las flores abiertas en su segundo día tuvieron menos néctar y polen que flores recién abiertas. Sin embargo, el néctar y polen en el segundo día fueron suficiente abundante para alentar las visitas de polinizadores potenciales. Patrones de abrir y cerrar a diario parecen bien apropriados para reducir el riesgo de polinizacíon inadecuada.

Key Words: Cactaceae, floral biology, floral longevity, *Opuntia engelmannii,* Sonoran Desert.

Flower longevity, the period of time from anthesis to senescence, interacts with other variables such as pollinator visitation and plant resources to control fruit set and seed production of many flowering plants (Primack 1985; Ashman and Schoen 1996). Large flowers, such as those typical of the Cactaceae, are presumably expensive to maintain for more than a single day and should open a second day only if there is ultimately a strong benefit to doing so, such as increased fruit set, seed production, or pollen donation (Primack 1985; Ashman and Schoen 1996). Proximate factors that influence longevity include transpirational water loss, respiration rate, and pollinator abundance (Primack 1985; Rosas and Pimienta 1986; Ashman and Schoen 1996).

Flowers of *Opuntia engelmannii* Salm-Dyck. (Engelmann prickly-pear), a shrubby platyopuntia widespread throughout the southwestern United States, are believed to last a single day (Parfitt and Pickett 1980; Turner et al. 1995), but floral longevity of two days has been reported for at least five other platyopuntias (Rosas and Pimienta 1986; Osborn et al. 1988; Schlindwein and Wittmann 1997). In these species, one-day flowers open in the morning and close permanently in late afternoon of the same day; two-day flowers open in the afternoon of their first day and close after several hours, then open again the following morning for several hours before senescing (Osborn et al. 1988; Schlindwein and Wittmann 1997). Both types last approximately the same amount of time, 6 to 12 hr (Osborn et al.

1988; Schlindwein and Wittmann 1997). The objective of this study was to describe temporal patterns of floral longevity for *O. engelmannii*. Specific questions asked were: (1) do individual flowers open on consecutive days, (2) is floral longevity consistent throughout the flowering season and among years, (3) is floral longevity limited by environmental or intrinsic factors, and (4) do pollen and nectar rewards vary with floral longevity?

Methods

Study Area

The study site was located at 720 m above sea level at the base of Tumamoc Hill (32°13′N, 111°05′W), an outlier of the Tucson Mountains, Pima County, AZ, USA. Study area vegetation is characteristic of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). In addition to *O. engelmannii,* dominant plants include *Cercidium microphyllum* (Torr.) Rose & Johnst., *Ambrosia deltoidea* (A. Gray) Payne, *Acacia constricta* Benth., *Larrea tridentata* (Moc. & Ses.) Cav., *Krameria grayi* Rose & Painter, *Carnegiea gigantea* (Engelm.) Britton & Rose, *Ferocactus wislizenii* (Engelm.) Britton & Rose and *Opuntia leptocaulis* DC. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter–early spring (November to March), an arid foresummer (April to June), a predictable summer monsoon (July to August), and a highly variable autumn (September to October). Maximum temperatures in summer often exceed 40°C. Minimum temperatures rarely drop below −6°C in winter. Although freezing nights can be frequent in winter, daytime temperatures always rise above 0°C.

Study Species

Opuntia engelmannii blooms once a year in April and May (Kearney and Peebles 1960; Turner et al. 1995). The hermaphroditic, yellow flowers are bowl-shaped and have a diameter of 6 to 9 cm (Benson 1982). Nectar accumulates in a short floral tube above the inferior ovary. Nectar production is high relative to other *Opuntia* spp. in the southwestern United States (Grant et al. 1979; McFarland 1983; Osborn et al. 1988; Neff and Simpson 1992). Anthers are numerous and produce copious pollen. As in many *Opuntia* species, the stamens are thigmotropic (Parfitt and Pickett 1980). Across the range of the species, flower visitors include several species of solitary bees (Grant and Hurd 1979; Grant and Grant 1979; Parfitt and Pickett 1980; Osborn et al. 1988). The anthophorids *Diadasia rinconis* Cockerell and *D. opuntiae* Cockerell are probably the most frequent pollinators in southern Arizona (Buchmann personal communication). Before the fruits ripen, beetles are common flower herbivores (Grant and Connell 1979).

Data Collection and Analysis

Two pilot studies were undertaken to determine whether individual flowers of *O. engelmannii* open on consecutive days. On 26 April 1995, 19 flower buds on seven plants and 21 open flowers on 10 plants were tagged and visited daily for the next seven days to monitor opening and closing dates. In 1997, additional flowers were marked and monitored on 18 April (n = 15 flowers) and 1 May (n = 129 flowers). Color and condition of tagged flowers were noted at each visit to determine how the appearance of flowers changed over time. In this and the following studies, flowers were tagged with numbered plastic or aluminum tags secured with straight pins inserted either into the base of the ovary or into the cladode beside the ovary. Mucilage quickly sealed the slight wound created by the pin. Flowers appeared unaffected by the pins.

Longevity in hours of one- and two-day flowers was monitored in 2003. Observations were made early in the flowering season (17 and 18 April) and about midway through the season (28 April to 2 May). Altogether, 192 flower buds on five plants were tagged on the day they opened for the first time. Buds were monitored every two hours throughout that day and the next from 0830 to 1630 hr (MST), and times of opening and closing were recorded. Independent t-tests were used to compare the longevity in hours of one- and two-day blossoms. A χ^2-test was used to determine whether opening time (morning versus afternoon) on the first day of bloom differed between one- and two-day flowers.

Proportions of one- and two-day flowers in the population were determined in 2000 and 2001 (n = 16 plants). In 2000, all flower buds (n = 580) were tagged at the start of the flowering season and monitored twice daily to determine longevity in days and also approximate time of opening (morning or afternoon). In 2001, the large number of flower buds (>4500) made it impracticable to individually tag and monitor all of them. Instead, the proportion of two-day flowers was estimated by making daily counts of total number of fresh flowers and number of flowers open for the second time on each sample plant. Counts were made in the morning, when second-day flowers (orange perianth) could be readily distinguished from fresh flowers (yellow perianth) (see Results). The proportion of second-day flowers was calculated as orange flowers of the current day divided by yellow flowers of the previous day. In addition, >200 flower buds were tagged and monitored twice daily in 2001 to determine approximate time of opening. Regression analysis was used to examine the influence of air temperature on the proportion of flowers opening a second day in 2000 or 2001. Maximum and minimum daily temperature were used separately as independent variables. Temperature data came from the University of Arizona, about 6 km distant.

To better understand daily and seasonal patterns of visitation, visits by potential pollinators were monitored throughout the flowering season in 2000 (n = 90 flowers) and 2001 (n = 261 flowers). Flowers were watched for 10 minutes, during which time the number of bee visitors was recorded. No attempt was made to identify the bees. Most observations were made between 0800 and 1300 hr (MST), when pollinators were very active. Beetles, which are not effective pollinators of cactus flowers (Grant and Connell 1979), were not included in these surveys.

Pollen and nectar contents of first- and second-day flowers were examined to see whether visitors can obtain rewards from older flowers. On 29 April 2001, mass of pollen was measured in freshly opened flowers and in flowers open for the second consecutive day. Twenty-four flowers on four plants were cut at 1030 hr and brought into the laboratory. Pollen was collected on sheets of waxed paper by holding flowers upside down over the paper and tapping them. Additional pollen was collected by dusting the anthers and petals with a small sable-hair brush. Pollen and paper were weighed together to the nearest 1.0 mg, then the waxed paper, cleaned of pollen, was weighed separately. The mass of pollen grains was calculated by subtraction.

Standing crop nectar in first- and second-day flowers was sampled in 1998. On 9 May, 11 May, and 12 May, flowers were tagged and classified according to color, condition, and time of opening as: (1) first day of bloom, opening in the morning (n = 32 flowers), (2) first day of bloom, opening in the afternoon (n = 24 flowers), or (3) second day of bloom, opening in the morning (n = 48 flowers). Nectar was sampled at hourly intervals on 9 May (0700 to 1100 hr), 11 May (0800 to 1600 hr), and 12 May (0700 to 1100 hr). Flowers were placed in plastic bags as they were removed from the plant, and the batch was refrigerated within several minutes. Nectar contents were measured in the laboratory within an hour of collection. Flower nectar was extracted using a bulb and uncalibrated glass pipette, then measured to the nearest 0.1 μl using a digital micropipette. Nectar values from all three days were pooled and averaged within hourly intervals.

Results

The pilot studies demonstrated that *O. engelmannii* flowers can open on two consecutive days, although many do not. Of 40 flowers buds and flowers tagged early in the flowering season in 1995, all lived for two days. In 1997, the proportions of two-day flowers were 78% on 18 April and 25% on 1 May. Fresh flowers had bright a yellow perianth; in addition, their stamens were pressed together, and little or no pollen could be seen on the stigmas or petals. As the day advanced, petals turned orange, stamens diverged, and pollen became liberally dusted on stigmas and petals. Flowers on their second day of bloom were also characterized by orange color, spreading stamens, and abundantly dispersed pollen. Flowers that opened in the morning typically senesced the same day; flowers that opened in the afternoon had a greater potential to bloom again the next day. From these findings, it was evident that: (1) a fresh flower opening in the morning is likely to be a one-day flower; (2) a fresh flower opening in the afternoon might be a one-day or a two-day flower; (3) a flower that has an orange perianth when it opens in the morning is a two-day flower on its second day of bloom. During the morning hours, therefore, it was possible to discern whether a flower was open for the first or second time and to predict its longevity with a fair degree of confidence.

In 2003, one-day flowers opened on average at 1100 hr (range = 0830 to 1230 hr) and closed 5.5 hr later at 1630 hr. Flowers that bloomed on two consecutive days were open altogether for an average of 12.2 hr. Their first day of bloom lasted about 6.5 hr, beginning around 1000 hr (range = 0830 to 1230 hr) and ending at about 1630 hr. On their second day, two-day flowers opened at 0830 hr without exception and closed shortly after 1400 hr. The difference in total longevity of one- and two-day flowers was significant ($t = 13.5$, $P = 0.001$). Note that daily phenology can be more variable than these data, gathered from four individuals over several days, would suggest. In other years, for example, some flowers opened for the first time as late as 1600 hr (personal observation).

In an analysis using all flowers tagged in 2003, one- and two-day flowers did not differ significantly in time of opening (morning versus afternoon) on the first day of bloom ($\chi^2 = 0.04$, df = 1, $P = 0.85$). This result was strongly influenced by the 28 flowers that bloomed for the first time on 17 April: all but two opened at 0830 hr, and all but three lasted two days. When these early-season flowers were dropped from the analysis, there was a significant difference in opening and closing times between one- and two-day flowers ($\chi^2 = 10.4$, df = 1, $P = 0.001$), with 70% of one-day flowers opening in the morning, and 71% of two-day flowers opening in the afternoon on their first day of bloom.

The proportion of flowers that opened on two consecutive days varied between years, being 0.8% in 2000 (4 of 483) and about 20% in 2001 (474 of 2368) (Fig. 1). In 2001, floral longevity was strongly associated with time of opening (morning versus afternoon): 93.7% of tagged flowers that opened in the morning (n = 111) turned out to be one-day flowers, and 56.9% of flowers that opened in the afternoon (n = 102) turned out to be two-day flowers ($\chi^2 = 64.1$, df = 1, $P = 0.001$). The number of two-day flowers in 2000 was too small for meaningful analysis; however, it is worth noting that

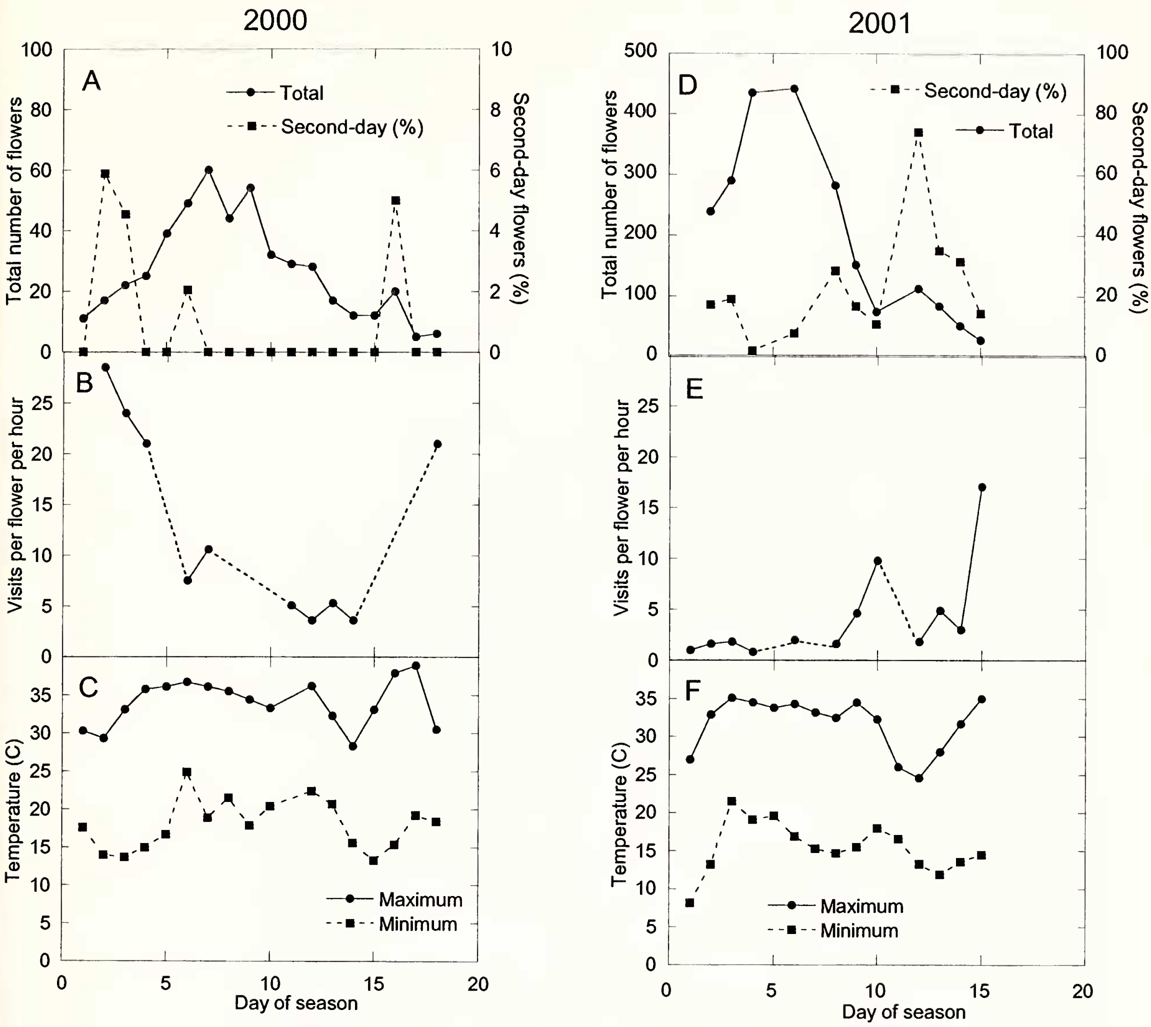

FIG. 1. The flowering season of *Opuntia engelmannii* in 2000 and 2001. Total number of flowers (circles) and proportion of two-day flowers (squares) in 2000 (A) and 2001 (D). Visits/flower/hour in 2000 (B) and 2001 (E); dotted lines show breaks in data collection. Daily maximum and minimum temperatures in 2000 (C) and 2001 (F).

88.8% of all flowers opened in the morning that year.

In 2001, there was a negative relation between temperature and the proportion of flowers that opened on two consecutive days. The relation was very strong for maximum temperature on the first day of bloom ($r^2 = 0.81$, $P < 0.001$) and not quite as strong for minimum temperature between the first and second days of bloom ($r^2 = 0.48$, $P = 0.01$) (Fig. 2a, b). In 2000, neither maximum nor minimum temperature were significantly related to proportion of two-day flowers, perhaps because most flowers opened in the morning; as noted above, flowers that open in the morning are likely to last only a single day.

Whether summarized by the day (Fig. 1) or by the hour (Fig. 3), visitation data were highly variable within and between years. Visits/flower/hr (±SD) in the morning were significantly higher in 2000 (11.2 ± 13.1) than in 2001 (4.2 ± 8.9) ($t = 5.59$, $P < 0.001$). The difference between years might have been related to intense competition among pollinators for flowers in 2000, a year of poor flower production, in contrast to 2001, a year of high flower production. Although afternoon observations were few, the trend in hourly visitation peaked in the morning and trailed off toward the afternoon (Fig. 3).

Mass of pollen grains (±SD) averaged 42 mg (±16) and 20 mg (±9) on the first and second days of bloom, respectively. The difference was significant ($t = 3.99$, $P = 0.001$) and undoubtedly reflected the time of day when flowers were harvested, about 1030 hr. At that time, flowers on their second day of bloom had been accessible to foraging bees for a longer time than recently opened flowers. The presence of pollen in second-day flowers indicated

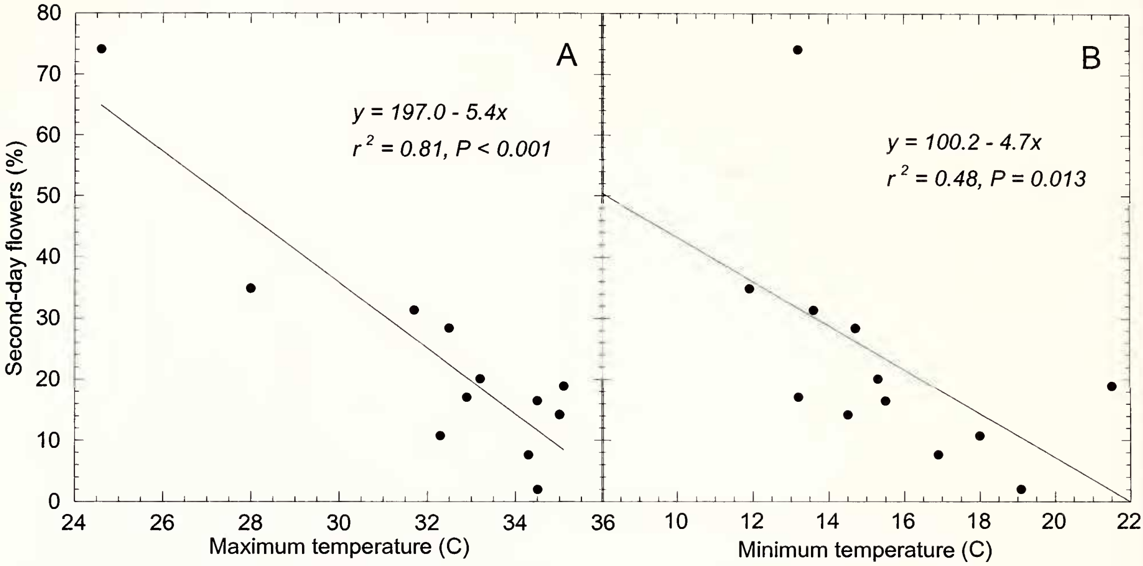

FIG. 2. Relation between air temperature and proportion of *Opuntia engelmannii* flowers that bloomed on two consecutive days in 2001. *X* axis represents maximum temperature on first day of bloom (A) or minimum temperature between first and second days of bloom (B).

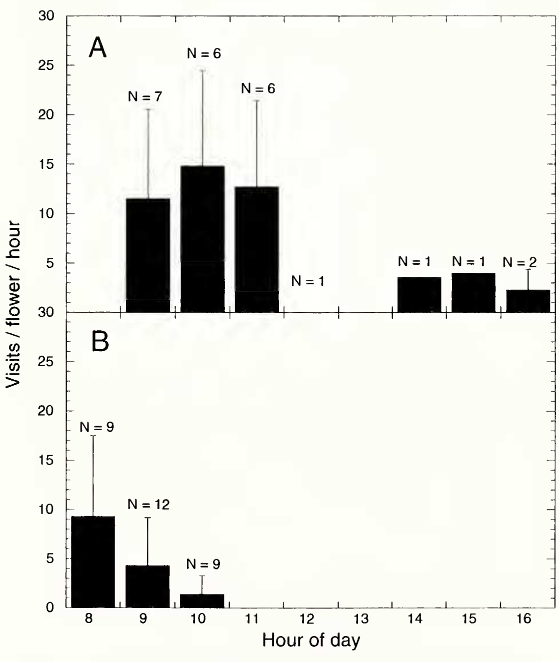

FIG. 3. Patterns of daily visitation (mean visits/flower/hr) by potential pollinators to flowers of *Opuntia engelmannii* in 2000 (A) and 2001 (B). Observations made throughout the flowering season were pooled and averaged within hourly intervals. N = days of observation. Error bars = 1 SD. In 2000, no observations were made from 0800 to 0900 hr or from 1300 to 1400 hr. In 2001, no observations were made after 1100 hr.

that some pollen remained at the end of the first day of bloom.

Day of bloom (first versus second) had a significant effect on standing crop nectar (ANOVA: F = 7.6, df = 2, 12, P = 0.007) (Fig. 4). On the first day of bloom, standing nectar crop averaged 22.6 μl/flower for flowers that opened in the morning and virtually the same, 21.9 μl/flower, for those that opened in the afternoon. Flowers on their second day of bloom contained significantly less nectar than either of the other categories, only 11.9 μl/flower (P < 0.02). Note that although the reward was relatively small, pollinators could find nectar in some second-day flowers.

DISCUSSION

Flowers of *O. engelmannii* opened on one or two consecutive days. Pollen mass and nectar volume were significantly lower on the second day, yet remained high enough to reward flower visitors and encourage a low level of visitation. Whether flowers lived for one or two days depended in part on air temperature, with a higher proportion of flowers opening a second time after relatively cool days and nights (Fig. 2a, b). Assuming that floral stomates were open during the day, as seems to be the case for *Ferocactus cylindraceus* (Engelm.) Orcutt (Nobel 1977), the negative effect of high daytime temperatures on flower longevity likely reflected loss of moisture through increased evapotranspiration. Respiration also increases with temperature, and it seems likely that high respiration rates on warm days and nights reduced flower longevity as well. Given relatively cool temperatures, some or many

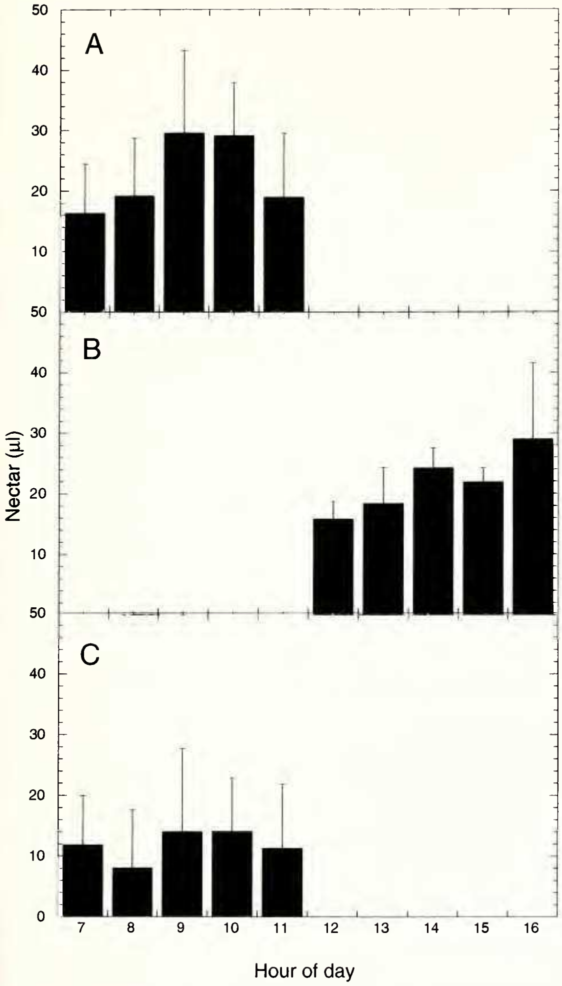

FIG. 4. Mean standing crop nectar of three phenophases of *Opuntia engelmannii* in 1998. (A) First day of bloom, flowers opening in the morning; (B) first day of bloom, flowers opening in the afternoon; (C) second day of bloom, flowers opening in the morning. Values represent the average amount of nectar measured in three to four flowers of each category at hourly intervals on three different days. Error bars = 1 SD.

flowers retained enough moisture to open two days in a row.

Another factor that determined how long flowers lived was time of opening. At mid-season in 2003, most (70%) two-day flowers opened in the afternoon, whereas most (71%) one-day flowers opened in the morning. In 2001, almost 94% of flowers that opened in the morning lasted a single day, and 57% of flowers that opened in the afternoon lived for two days. On their first day, two-day flowers opened about the same time as one-day flowers, but on their second day, two-day flowers typically opened 1.5 to 2.5 hours earlier than one-day flowers.

Patterns of daily opening and closing appear well suited to reducing the risk of poor or no pollination. Emergence and abundance of the primary pollinators, *Diadasia rinconis* and *D. opuntiae*, varies considerably among years (Ordway 1984; Ordway 1987; Neff and Simpson 1992). As a result, pollination might be inadequate in years when the bees emerge before or after peak bloom, or when their populations are small relative to the number of flowers available (Neff and Simpson 1992). Early in the flowering season, when temperatures tend to be cooler, most *O. engelmannii* flowers open in the morning and live for two days, perhaps increasing the likelihood of pollination when the presence of pollinators is uncertain. Later in the season, when days are warmer, pollinators are more abundant. They are active throughout the day (Ordway 1984), but typically make many more flower visits in the morning than in the afternoon (Fig. 2). One-day flowers, by opening in the morning, receive frequent visitation but are also likely to be spent by the end of the day as a consequence of higher temperatures. Two-day flowers, by opening after noon on their first day, receive few visits then, but, by opening well before all other flowers on their second day, gain a virtual monopoly on early morning visitation. The main risk to this strategy is that very warm temperatures on the first day might preclude a second day of bloom.

These and other hypotheses, such as maximization of male or female fitness, require careful testing; in the meantime, it is evident that by controlling accessibility of flowers to pollinators, temperature and time of opening might have profound implications for the reproductive biology of *O. engelmannii.*

ACKNOWLEDGMENTS

I am indebted to S. P. McLaughlin and L. Slauson for many helpful comments on the manuscript.

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